SEED DISPERSAL IN *CEANOTHUS CUNEATUS* AND *C. LEUCODERMIS* IN A SIERRAN OAK-WOODLAND SAVANNA

RAYMOND A. EVANS
USDA/ARS, 920 Valley Road, Reno, NV 89512

HAROLD H. BISWELL
Department of Forestry, University of California, Berkeley 94720

DEBRA E. PALMQUIST
University of Nevada, Reno 89512

ABSTRACT

Seed dispersal of *Ceanothus cuneatus* and *C. leucodermis* was studied in an oak-woodland community in the central Sierra Nevada of California. As the capsule of *Ceanothus* (usually containing three seeds) matures and dries, it opens with force and ejects its seeds at varying distances. Seed-casting, in relation to date, showed a skewed polynomial distribution that peaked early in July and gradually tapered off. The active seed-casting period lasted two weeks in the one year of study. Phenology of fruit ripening, temperature, and humidity were related directly to time and rate of seed-casting. About one-third of the seeds fell beneath the canopy, whereas the remainder were cast away from the shrub in an exponential density distribution. Forty-two percent of the seeds (average density of 2850 m^{-2}) fell at the edge of the shrub and 1.9% (average density of 10 m^{-2}) at 9 m. The probabilities that seeds would be cast within specific distances from the shrub were 29% (at the edge of the shrub to 2 m), 33% (4–6 m), and 21% (8–9 m).

Ceanothus comprises 55 species restricted to North America, and most are found along the Pacific coast of the United States (Reed 1974). Californian species are ecologically diverse and, among other communities, are found in the chaparral, oak-woodland savannas, and lower coniferous forests of the Sierra Nevada. *Ceanothus* is important as wildlife feed and habitat, and because of its nitrogen-fixing properties also is important in soil development and conservation (Zavitkovski and Newton 1968, Youngberg and Wollum 1976). Among the oak-woodland savannas of the Sierra Nevada foothills, *C. cuneatus* and *C. leucodermis* are considered weeds to livestock producers because they compete with the herbaceous vegetation and reduce the yield of forage for cattle (Biswell 1974).

As the capsule of *Ceanothus* matures and dries, it opens with force and ejects the seeds to varying distances from the parent shrub. Explosively dispersed seeds have been reported for other genera, including *Dendromecon, Oxalis, Viola, Phlox, Geranium, Alstroemeria, Lupinus, Impatiens, Millettia,* and *Hura* (Swaine and Beer

MADROÑO, Vol. 34, No. 4, pp. 283–293, 1987

1977). Individuals of these genera cast their seeds 1–45 m, depending on species and size of plant. Little is known about the advantages of explosive seed dispersal in terms of seed germination or plant establishment. Many questions remain unanswered about the adaptive advantages conferred on a species by investment in dispersal structures (Howe and Smallwood 1982).

The primary objectives of this study were to investigate seed dispersal patterns of *C. cuneatus* and *C. leucodermis* in order to more fully understand seed bank characteristics that appear advantageous to the establishment of new plants, and to examine seed dispersal patterns in light of theoretical models of explosively dispersed seeds (Beer and Swaine 1977) and the theoretical distribution and probability distributions of seeds (Peart 1985).

Methods

Studies were conducted in a California oak-woodland savanna community, situated in the foothills of the central Sierra Nevada, 70 km northeast of Fresno, at 910 m and with an average rainfall of 760 mm. Dominant tree species are *Pinus sabiniana, Quercus douglasii, Q. wislizenii,* and *Aesculus californica,* and dominant shrub species are *Ceanothus cuneatus* and *C. leucodermis.* An understory of herbaceous plants includes the annual grasses, *Bromus mollis, B. diandrus, B. rubens, Avena barbata, A. fatua,* and *Festuca* spp.; and the broadleaf plants, *Erodium botrys, E. cicutarium, Medicago polymorpha,* and *Trifolium* spp.

Eight representative plants of *Ceanothus cuneatus* and *C. leucodermis* were selected in the study area (*C. cuneatus,* 1–3.5 m tall and *C. leucodermis,* 2–4 m tall; Munz 1973). Transects 10 m long and 0.6 m wide, radiating out in eight compass directions from two large shrubs, one of each species, were cleared of herbaceous vegetation and plant litter (Fig. 1). One meter intervals along the transects were marked by large nails beginning at the edge of the shrub canopy. There was one sampling point beneath the canopy on each transect positioned 0.3 m inside the canopy edge. On smaller shrubs, one to four transects were made along compass directions radiating out from each shrub, based on the proximity of adjacent shrubs and terrain. These transects were cleared and marked in a similar fashion to the large shrubs. No transects were made adjacent to neighboring shrubs to avoid measuring areas of overlap of seed dispersal from two or more shrubs.

Sampling for seed dispersal consisted of counting seeds within a 0.1 m^2 frame every other day during the active casting period. After seeds were counted, the transects were swept clean with a whisk broom. The counts were made in early evening or early morning when seeds were not dehiscing. To minimize seed predation, ants

FIG. 1. *Ceanothus cuneatus* with cleared transects radiating out from the shrub in eight cardinal directions.

were poisoned in the transect areas. No indication of seed predation by rodents or birds was noted during the course of the study.

When the capsules of *Ceanothus* burst open and dehisce their seeds an audible pop is heard. At the height of casting on 20 July, seed dehiscing on the large shrubs of both species was monitored every 30 minutes from 0700–2130 hr by counting the number of pops heard by an observer standing close to the individual shrub for three 60 second intervals. At the same time, measurements of relative humidity and temperature were made using a sling psychrometer. Seasonal weather data were taken from the nearest station, North Fork Ranger Station, located 16 km south of the study area at 800 m.

Results were analyzed statistically by ANOVA with Duncan's multiple range test to determine differences in seed density in relation to compass direction. Correlation and curvilinear regression techniques were used to portray and analyze seed dispersal relative to distance from the shrub canopies and to calendar date.

RESULTS

Seed-casting in relation to date. Seed-casting for both *C. cuneatus* and *C. leucodermis* occurred from 13 July to 11 August 1952. The

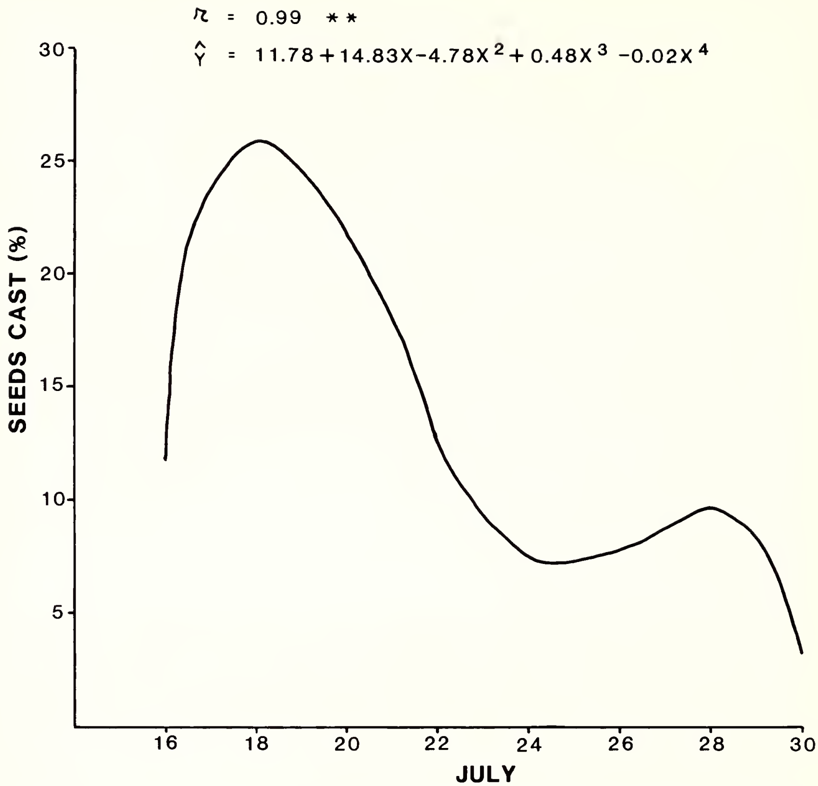

Fig. 2. Fourth-degree polynomial distribution curve of percentage of *Ceanothus cuneatus* seeds cast in relation to calendar date. Multiple correlation coefficient (r) is significant at $p \leq 0.01$.

period of active seed-casting, when more than 95% of the observed total seeds were dispersed, lasted 14 days (16–30 July). Average maximum and minimum daily temperatures during active seed casting were 35.7 ± 2.1°C and 15.1 ± 2.5°C, respectively. Rain showers occurred 25 July (2.3 mm) and 30 July (2.5 mm). Partly cloudy weather accompanied the showers, which increased the humidity and decreased air temperatures during these periods.

Maximum seed-casting occurred on 18 and 20 July (two and four days after the active seed-casting period began) for *C. cuneatus* and *C. leucodermis,* respectively (Figs. 2, 3). Seed casting in relation to date formed a skewed fourth-degree polynomial distribution in which the numbers of seeds cast increased rapidly from the initiation of casting and decreased gradually over the following 10–12 days. In *C. cuneatus,* a marked decrease in seed dispersal was noted during

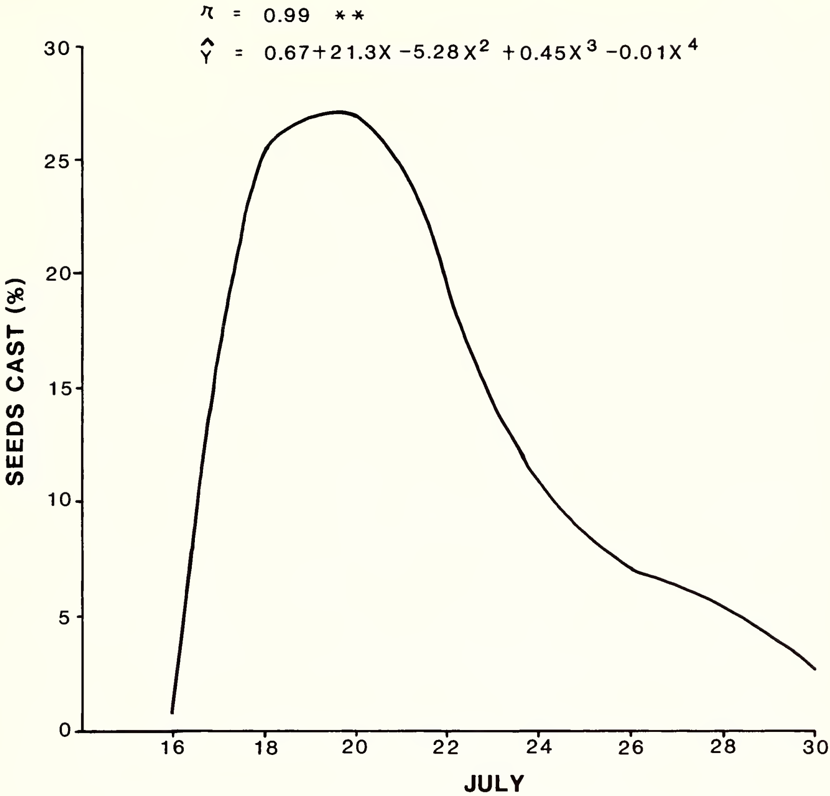

FIG. 3. Fourth-degree polynomial distribution curve of percentages of *Ceanothus leucodermis* seeds cast in relation to calendar date. Multiple correlation coefficient (r) is significant at $p \leq 0.01$.

the period of higher humidity and rainfall toward the end of active seed casting and then a subsequent increase with higher temperatures and lower humidity (Fig. 2). In *C. leucodermis,* this response was similar, but of less magnitude (Fig. 3).

Seed-casting in relation to time of day. On 20 July, seed casting of both species occurred from 0930–2130 hr (Fig. 4). Seed-casting in *C. cuneatus* reached a maximum at 1200 hr and continued at a high level (20/min being counted) until 1700 hr. Seed-casting in *C. leucodermis* increased to a high level at 1230 hr and reached similar maxima at 1730 and 1830 hr. Total seeds cast on 20 July was almost identical for monitored shrubs of both species (Figs. 2, 3). At the onset of seed-casting, temperature was 27°C and relative humidity (RH) 30%. In the most active period of seed-casting, temperatures

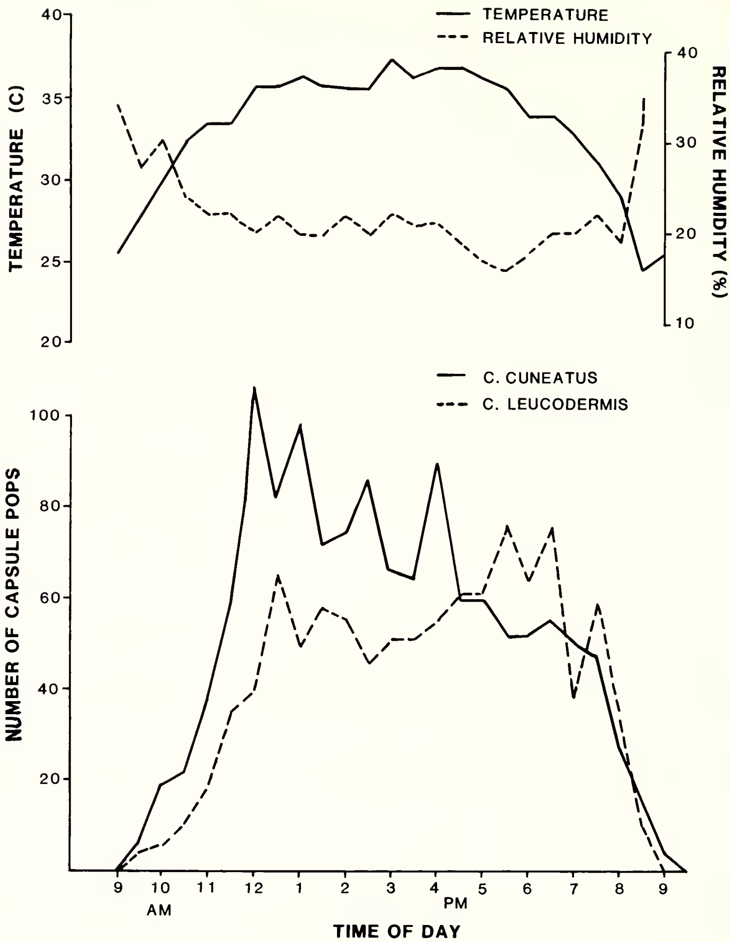

FIG. 4. Number of capsule pops of *Ceanothus cuneatus* and *C. leucodermis* per three minute period and air temperature and relative humidity for each one-half hour on 20 July.

ranged from 35–38°C with RH from 15–20%. At cessation of casting, temperature was 25°C and RH was 37%.

Seed-casting in relation to distance from shrub. Of the total seeds cast, 32% and 36% fell beneath the shrub canopy of *C. cuneatus* and *C. leucodermis,* respectively. This presumably resulted from seeds striking branches or leaves or because the seed capsules were oriented downward or inward. The remainder of seeds cast by both species formed an exponential density distribution from a high of 42% at the edge of the shrub to 1.9% at 9 m from the shrub (Fig. 5). Seed

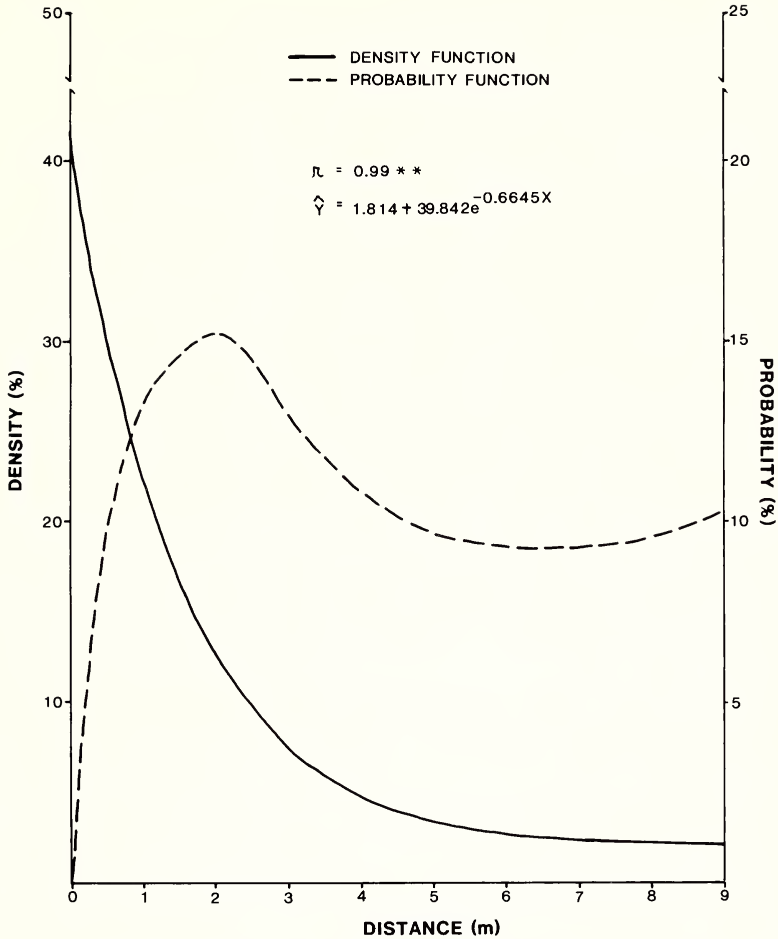

FIG. 5. Density and probability functions of seed-casting distribution of *Ceanothus cuneatus* and *C. leucodermis* in relation to distance from edge of the parent shrub. Data for both species are combined. Multiple correlation coefficient (r) of the density function is significant at $p \leq 0.01$. Probability function should be interpreted as a measure of probability of a seed landing within a specific distance range from edge of the parent shrub.

densities averaged 2850 m^{-2} at the edge of the shrub to 10 m^{-2} at 9 m. Overall dispersal patterns of different shrubs were consistent in both species and were not significantly different ($p \leq 0.05$) between species (Table 1). Highest seed densities, those near the shrubs, agreed with densities reported by Keeley (1977) for *C. leucodermis.*

The probability of a seed escaping from the parent plant and landing within a specific distance range was derived by P(r) =

TABLE 1. CALCULATED SEED DENSITIES OF *Ceanothus cuneatus* AND *C. leucodermis* AT VARIOUS DISTANCES FROM THE PARENT SHRUBS WITH CONFIDENCE INTERVALS DERIVED FROM MULTIPLE REGRESSION. Correlation coefficient for multiple regression = 0.99; n = per 0.1 m^2.

Distance from edge of shrub (m)	*C. cuneatus* (n)	*C. leucodermis* (n)	Confidence interval p = 0.05
0	273	277	16
1	163	167	10
2	92	96	8
3	53	57	8
4	31	35	8
5	19	23	8
6	16	8	9
7	8	12	9
8	6	10	9
9	5	9	9

$2\pi rD(r)dr$ (Peart 1985), where P(r) = probability of a seed escaping to an angular area at distance (r) from the point of release; D(r) = a density-dispersal function based on actual sampling data of the two species; and dr = sample size of 0.1 m. Results indicated that the probability of a seed landing within specific distance ranges from the parent shrub varied from 29% (edge of the shrub to 2 m), to 33% (4–6 m), and to 21% (8–9 m) (Fig. 5).

Seed-casting in relation to direction from shrub. Over the active period of casting, most *C. cuneatus* seeds were cast in a southwesterly direction and fewest in a westerly direction. Early in the casting period and at maximum seed dispersal more seeds were cast to the north and east, whereas later in the casting period most seeds were cast in the southwesterly direction. In *C. leucodermis,* most seeds were cast in a southeasterly direction and fewest were cast in a westerly direction. Most seeds were cast to the southeast during the 10 days of most active seed dispersal. In both species, fewer seeds were cast to the west throughout the dispersal period (Table 2).

DISCUSSION

Seed-casting in *Ceanothus cuneatus* and *C. leucodermis* occurs during a short but active period (14 days in this study), when the capsules ripen and expel their seeds (usually three per capsule) to a distance of 9 m or more. Seeds are dispersed mainly beneath or near parent shrubs, but explosive dispersal permits a wider distribution of some seeds. Both diurnal and seasonal trends of seed-casting seem to indicate that specific thresholds of temperature and moisture were critical for seed-casting in *Ceanothus.* Our results suggest that commencement and rate of seed-casting are functions of the phenological

TABLE 2. PERCENTAGE OF SEEDS CAST IN DIFFERENT DIRECTIONS FROM PARENT SHRUBS OF *Ceanothus cuneatus* AND *C. leucodermis*. Values followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's multiple range test. All comparisons are made horizontally within species.

Species	Compass direction							
	n.	ne.	e.	se.	s.	sw.	w.	nw.
	Percent							
C. cuneatus	10.7ab	10.9ab	13.6ab	12.6ab	15.0ab	15.6a	7.6b	14.0ab
C. leucodermis	12.9ac	10.0bc	8.8c	15.9a	15.0ab	13.1a–c	10.0bc	14.3ab

stage of fruit ripening and of the temperature and relative humidity as they affect plant moisture status.

Ceanothus seeds require relatively high temperatures (70–100°C) for germination (Reed 1974). Most germination and seedling establishment is associated with fire (Quick and Quick 1961, Schlesinger and Gill 1978). Between fires, large seed banks of *C. cuneatus* and *C. leucodermis* beneath and around shrubs can accumulate in the Sierran oak-woodland savanna.

Effects of the interaction of seed dispersal at varying distances from the parent shrubs and seed mortality in relation to fire temperature as influenced by type (shrub vs. herbaceous) and amount of fuel create a mosaic of safe sites (Harper et al. 1965) for seed germination and plant establishment. Seedling establishment of *Ceanothus* in relation to competition from herbaceous species (Schultz et al. 1955) that grow among shrubs increases heterogeneity of the seed bank in terms of safe sites and restricts opportunities for successful establishment of seedlings. Furthermore, wide dispersal of long-lived seeds of *Ceanothus* increases the probability for establishment of new plants by reducing the effects of seed predation by insects, predation and herbivory by rodents, and intraspecific seedling competition (Peart 1985).

Acknowledgments

The senior author acknowledges the tireless efforts and exceptional ability of his wife, Dorthea B. Evans, in assisting in the field sampling of the study. I also thank her for encouragement and inspiration during all phases of the study.

Literature Cited

Beer, T. and M. D. Swaine. 1977. On the theory of explosively dispersed seeds. New Phytol. 78:681–694.

Biswell, H. H. 1974. Effects of fire on chaparral. *In* T. T. Kozlowski and C. E. Ahlgren, eds., Fire and ecosystems, p. 321–364. Academic Press, New York.

Harper, J. L., L. T. Williams, and G. R. Sagar. 1965. The behavior of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants. J. Ecology 539:273–286.

Howe, H. F. and J. Smallwood. 1982. Ecology of seed dispersal. Ann. Rev. Ecol. Syst. 13:201–228.

Keeley, J. E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecology 58:820–829.

Munz, P. A. 1973. A California flora with supplement. Univ. California Press, Berkeley.

Peart, D. R. 1985. The quantitative representation of seed and pollen dispersal. Ecology 66:1081–1083.

Quick, C. R. and A. S. Quick. 1961. Germination of *Ceanothus* seeds. Madroño 16:23–30.

Reed, M. J. 1974. *Ceanothus*. *In* C. S. Schopmeyer, tech. coord., Seeds of woody plants in the United States, p. 284–290. Agriculture Handbook No. 450, Forest Service, U.S.D.A., Washington, DC.

Schlesinger, W. A. and D. S. Gill. 1978. Demographic studies of the chaparral shrub, *Ceanothus megacarpus* in the Santa Ynez mountains, California. Ecology 59:1256–1263.

Schultz, A. M., J. L. Launchbaugh, and H. H. Biswell. 1955. Relationship between grass density and brush survival. Ecology 36:226–238.

Swain, M. D. and T. Beer. 1977. Explosive seed dispersal in *Hura crepitans* L. (Euphorbiaceae). New Phytol. 78:695–708.

Youngberg, C. T. and A. G. Wollum II. 1976. Nitrogen accretion in developing *Ceanothus velutinus* stands. Soil Sci. Soc. Amer. Proc. 40:108–112.

Zavitkovski, J. and M. Newton. 1968. Ecological importance of snowbrush *Ceanothus velutinus* in the Oregon Cascades. Ecology 49:1134–1145.

(Received 14 Apr 1986; revision accepted 9 Mar 1987.)

ANNOUNCEMENT

The 1987 Jesse M. Greenman Award

The 1987 Jesse M. Greenman Award has been won by Geoffrey A. Levin for his publications "Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus", "Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). II. Phenetic Analysis", which appeared in the *Annals of the Missouri Botanical Garden,* volume 73, number 1, and "Systematic Foliar Morphology of Phyllanthoideae (Euphorbiaceae). III. Cladistic Analysis", which was published in *Systematic Botany,* volume 11, number 4. This series of papers is derived from a Ph.D. dissertation from the University of California, Davis, under the direction of Drs. James A. Doyle, Grady L. Webster, and Jack A. Wolfe. Dr. Levin uses a large set of characters (in this case leaf characters) to address questions of systematic relationships and phylogeny at higher taxonomic levels, using the results from both phenetic and cladistic analysis to evaluate a more traditional classification system, and to identify genera or groups of genera whose position and relationship are not clear and, therefore, are in need of additional study.

The Award is named for Jesse More Greenman (1867–1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of $250 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation that was published during the previous year. Papers published during 1987 are now being considered for the 20th annual award, which will be presented in the summer of 1988. Reprints of such papers should be sent to: Greenman Award Committee, Division of Research, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, U.S.A. In order to be considered for the 1988 award, reprints must be received by 1 June 1988.